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A revision of the species of *Hypocalymma* (Myrtaceae: Chamelaucieae) with smooth or colliculate seeds

Barbara L. Rye^{1,3}, Peter G. Wilson² and Greg J. Keighery¹

¹Western Australian Herbarium, Department of Parks and Wildlife, Locked Bag 104, Bentley Delivery Centre, Western Australia 6983 ²National Herbarium of New South Wales, Royal Botanic Gardens and Domain Trust, Mrs Macquaries Road, Sydney, New South Wales 2000 ³Corresponding author, email: Barbara.Rye@dpaw.wa.gov.au

Abstract

Rye, B.L., Wilson, P.G. & Keighery, G.J. A revision of the species of *Hypocalymma* (Myrtaceae: Chamelaucieae) with smooth or colliculate seeds. *Nuytsia* 23: 283–312 (2013). Most members of the south-western Australian genus *Hypocalymma* (Endl.) Endl. have seeds with a shallowly to very deeply pitted testa. Two small groups of species, both revised here, differ in having a smooth or colliculate testa. Both groups occur in humid environments in the extreme south-west of Western Australia and show vegetative adaptations consistent with this habitat preference. The larger group, *Hypocalymma* sect. *Cardiomyrtus* Schauer, is reinstated. A new combination, *H. minus* (Strid & Keighery) Keighery, is made, bringing the total species recognised to five, and lectotypes are selected for two synonyms, *H. boroniaceum* F.Muell. ex Benth. and *H. hypericifolium* Benth. The other group is extremely rare, consisting of the possibly extinct species *H. connatum* Strid & Keighery, and a new species known from a single population, *H. verticillare* Rye. The latter group, named here as *Hypocalymma* sect. *Verticilla* Rye, is readily distinguished by its 3-ridged young stems and consistently whorled leaves, and the new species is unusual in having extreme differences in the sizes of the anthers on different stamens within each flower. Molecular data indicate that sect. *Verticilla* is sister to sect. *Cardiomyrtus*. Evidence of taxonomic relationships is also presented from studies of hybridisation and insect associations.

Introduction

Hypocalymma (Endl.) Endl. is a moderate-sized, myrtaceous genus belonging to the tribe Chamelaucieae DC. Although relatively restricted in its distribution, occurring only in the South-west Botanical Province of Western Australia (see Rye 2013: Figure 5C), the genus is morphologically diverse. Schauer (1844) and Bentham (1867) recognised three sections, but Strid and Keighery (2002) decided not to use sections for the more varied and numerous species of Hypocalymma known by that stage.

Recent molecular studies using four chloroplast regions (Lam *et al.* 2002; Wilson *et al.* 2004), have suggested that the smallest of Schauer's three sections, *Hypocalymma* sect. *Cardiomyrtus* Schauer, should be recognised as a distinct group. Several morphological differences that were uncovered during the current study, especially a difference in the seed testa, also suggest that sect. *Cardiomyrtus* should be recognised. While most species of *Hypocalymma* have a shallowly to deeply pitted testa (see Sweedman & Merritt 2006: 126; Rye & Trudgen 2008: Figure 3C), members of sect. *Cardiomyrtus* have a smooth or colliculate testa.

A second group of smooth-seeded *Hypocalymma* species, treated here as the new section *Verticilla* Rye, has such a distinctive morphology that its generic placement has been unclear. The first herbarium specimen belonging to this plant group was taken from a species displayed in a wildflower show in Perth in September 1935. This specimen was identified by Charles Gardner on the label as '*Baeckea Hypocalymma* or *Astartea* a new plant' after he had failed to find any match for it at Kew. No further material came to light and the taxon remained in obscurity for more than sixty years until it was included in a cladistic study (Foster 1996) and later described as *H. connatum* Strid & Keighery (Strid & Keighery 2002). Many of the leaves and almost all of the flowers and fruits had fallen from the stems of the single specimen of *H. connatum*; this may have contributed to two incorrect character states, *viz.* quadrangular stems and paired flowers, being given in the protologue. In fact, *H. connatum* is unusual in having three-angled stems, with leaves borne in alternating whorls of three and the number of flowers produced at each node varying from one to three.

A full revision of *Hypocalymma* sections *Cardiomyrtus* and *Verticilla* is presented here. In the remainder of the genus, i.e. the taxa with pitted seeds, most species seem to form a cohesive group that includes the type species (i.e. sect. *Hypocalymma s. str.*); however, a few atypical species need further study to determine whether they should be maintained within sect. *Hypocalymma s. lat.* or placed in a new section.

Methods

Measurements were taken from well pressed, herbarium specimens, using the largest leaves on each specimen and taking care to measure the inflorescence and floral organs when they were fully mature. Few specimens are cited here because extensive lists of specimens have already been published in Strid and Keighery (2002). Some new or recently incorporated specimens are cited and also a few specimens with recently altered identifications.

Multiple images of seeds and other organs were taken with a Nikon Digital Head (DS-5M) controlled by a DS Camera Control Unit (DS-L1) and a montage of the images was collated using the Synopics Auto-Montage Pro Version 5.03.0061 software.

Sectional classification of Hypocalymma

Taxonomic history

Hypocalymma (Endlicher 1837, 1840) originally consisted of the two species now known as H. angustifolium (Endl.) Schauer and H. robustum (Endl.) Lindl., the latter of which was recently selected (Rye 2010) as the lectotype for the genus. Schauer (1844) established three sections in the genus. Section Eucalymma Schauer nom. illeg. [= sect. Hypocalymma], contained the lectotype H. robustum as well as H. asperum Schauer and H. strictum Schauer. Another section, Astrocalymma Schauer, consisted of H. angustifolium and H. scariosum Schauer. Schauer (1844) based his third section, Cardiomyrtus, on the single species H. cordifolium Lehm. ex Schauer and distinguished it from the other two sections partly by its distinctly pedunculate flowers. At that time, when there were so few species of Hypocalymma known, each section could be readily defined on the basis of the number of loculi and ovules per loculus in the ovary as follows:

- 1. Sect. *Eucalymma* [= sect. *Hypocalymma*] with 2 loculi and 3 ovules per loculus.
- 2. Sect. Astrocalymma with 3 loculi and 1 ovule per loculus.
- 3. Sect. Cardiomyrtus with 3 loculi and 2 ovules per loculus.

Turczaninow (1862) named two additional sections for species that had 3-locular ovaries but these groups were not validly published as they did not include any diagnostic description. Section *Calocalymna* Turcz. *nom. inval.* was based on *H. speciosum* Turcz., a species with deep pink-purple flowers, a superior ovary and colliculate seeds. The other section, *Chrysocalymna* Turcz. *nom. inval.*, had pitted seeds; it contained the yellow-flowered species currently known as *H. linifolium* Turcz. and *H. xanthopetalum* F.Muell.

By the time Bentham (1867) published his treatment of *Hypocalymma* in *Flora Australiensis*, 13 of the species now recognised had been named. The increased range of morphological variation in the additional species included higher ovule numbers, 6–12 per loculus, in two species that Bentham added to section *Cardiomyrtus*. In modifying the infrageneric classification to accommodate the new species, Bentham used extra characters, including the degree of development of ridges on the ovary summit and whether or not the style was inserted in a cavity.

Niedenzu (1893) expanded the circumscription of *Hypocalymma* to include *Rinzia* Schauer, placing its species in sect. *Cardiomyrtus*, but subsequent authors mostly followed Bentham's placement of *Rinzia* as a section of *Baeckea* L. In a paper reinstating *Rinzia*, Trudgen (1986: 416, 418) considered *Hypocalymma* to be a close relative that differed in its 'more numerous and exserted stamens', and basifixed anthers apparently 'developed through the fusion of the filament to the lower part of the anthers'.

Foster (1996) raised the possibility that a new genus might be needed for the species now named *H. connatum*. His cladistic analysis supported the genus *Hypocalymma s. lat.* and placed *H. connatum* close to *H. cordifolium*, but he noted that characters not used in the analysis suggested that *H. connatum* was very distinctive.

Although Strid and Keighery (2002) did not recognise any sections in their revision of *Hypocalymma*, their systematic ordering of the species corresponded with the species groups recognised here. They placed 17 species with pitted seeds first, followed by the four species of sect. *Cardiomyrtus sensu* Bentham (1867) and then *H. connatum*. The last two of the 17 species with pitted seeds—*H. puniceum* C.A.Gardner and *H. melaleucoides* C.A.Gardner ex Strid & Keighery—were atypical of the genus in having the stamens much shorter than the petals. Three undescribed taxa—*H. puniceum* subsp. Cadoux (H. Demarz 10533), *H.* sp. Cascade (R. Bruhn 20896) and *H.* sp. Lake King (R.W. Purdie 3936)—also have a low stamen length to petal length ratio. These five taxa are referred to here as the *H. puniceum* group.

Molecular sequencing

Recent molecular studies of several chloroplast regions (Lam *et al.* 2002; Wilson *et al.* 2004) indicate that *Hypocalymma* is much more closely related to *Astartea* DC. and *Cyathostemon* Turcz. than to *Rinzia*. Six species of *Hypocalymma* were sampled, three with pitted seeds and three with smooth or colliculate seeds. The three species with pitted seeds (one representative of each of the sections

Astrocalymma, Chrysocalymna nom. inval. and Hypocalymma) were placed together. However, the other three species sampled (two representatives from sect. Cardiomyrtus and one from sect. Calocalymna nom. inval.) formed a separate clade from that containing the taxa with pitted seeds.

Analysis of an expanded molecular dataset, with sequences from the nuclear ETS region added to the existing chloroplast data, was included in a presentation at the 2011 International Botanical Congress (abstract published as Wilson & Heslewood 2011). The nine species used in this analysis (Figure 1) are more diverse, including one representative of the *H. puniceum* group and one of the new section, *Verticilla*. Phylogenetic analysis of these nine species indicates that *Hypocalymma* is a monophyletic group, but with weak jackknife (jk) support (64% jk). The group divides into two moderately, to well, supported clades. In the first, with 84% jk support, the new section, *Verticilla*, is sister to a strongly supported (97% jk) clade comprising three species of sections *Cardiomyrtus* and '*Calocalymna*'. The second branch has *H. puniceum* very strongly supported (100% jk) as sister to another robust clade representing sections *Astrocalymma*, '*Chrysocalymna*' and *Hypocalymma*. The topology of this part of the phylogeny suggests that further investigation might result in the *H. puniceum* group being treated as a distinct section

Hybridisation

Strid and Keighery (2002) noted the existence of natural hybrids between the widespread *H. angustifolium s. lat.* (sect. *Astrocalymma*) and a variety of other species with pitted seeds, including *H. robustum* (sect. *Hypocalymma*). The most extensive case of hybridisation (M. Trudgen pers. comm., K. Thiele pers. comm.) occurs at localities where *H. tetrapterum* Turcz. co-exists with the flat-leaved variant of the *H. angustifolium* complex, with the production of hybrid swarms. The informal name *Hypocalymma* sp. Cataby (G.J. Keighery 5151) applies to these hybrids.

The Botanic Gardens and Parks Authority has attempted to cross several large-flowered species (belonging to sect. *Cardiomyrtus* and the *H. puniceum* group) with *H. angustifolium* (sect. *Astrocalymma*) but no seed set resulted (D. Growns pers. comm.).

No natural hybrids have been recorded for species with smooth to colliculate seeds, either in the rare instances when they co-occur or the perhaps more numerous occasions where they occur with pitted-seeded species.

Conclusion

All known cases of natural hybridisation occur either within or between the three named sections with pitted seeds, *Astrocalymma*, '*Chrysocalymna*' and *Hypocalymma*, and there do not appear to be any clear morphological differences to define these three groups. It is concluded from this evidence, and also from the molecular data, that *Astrocalymma* and '*Chrysocalymna*' should be treated as synonyms of sect. *Hypocalymma*. However, both the hybridisation data and the molecular data suggest that the *H. puniceum* group is distinctive.

Among the taxa with smooth to colliculate seeds, the molecular data indicate that sect. 'Calocalymna' should be considered a synonym of sect. Cardiomyrtus but that the Verticilla group is likely to be distinct. Morphological differences that support the recognition of these two groups as separate sections are outlined below.

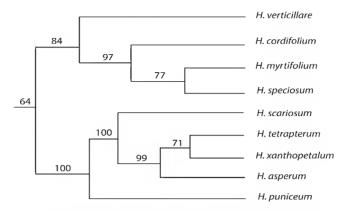


Figure 1. Preliminary phylogeny of *Hypocalymma* (from Wilson & Heslewood (2011), unpublished analysis of tribe Chamelaucieae) showing jackknife supports.

Morphology

The morphology of the new section *Verticilla* is compared with that of the previously named sections *Cardiomyrtus* and *Hypocalymma* in Table 1. Note that the *H. puniceum* group is excluded from the character states given in Table 1 for sect. *Hypocalymma* as it appears to be very distinctive, differing in having only one flower per axil, pedicels up to 2 mm long and seeds reaching a slightly higher maximum length of 2.5 mm. The main distinguishing character of the *H. puniceum* group, i.e. large petals that greatly exceed the stamens, is not listed in the table.

As can be seen from Table 1, sections *Cardiomyrtus* and *Verticilla* differ from the typical section mainly in their leaf, inflorescence and seed characters. They also differ from one another in their stems, leaves, inflorescence and androecium. Sect. *Verticilla* resembles the genus *Cyathostemon* in its androecium and in having solitary, distinctly stalked, axillary flowers. However, the flowers in sect. *Verticilla* have a long peduncle exceeding the pedicel whereas in *Cyathostemon* the peduncle is usually much reduced and greatly exceeded by the pedicel.

Habit. Sections Cardiomyrtus and Verticilla consist of small or moderate-sized shrubs, mostly less than 1 m high, although H. phillipsii Harv. may occasionally reach a height of about 1.5 m and the height of H. connatum is unknown. Two species, H. cordifolium and H. verticillare, are single-stemmed at the base, whereas the three species of sect. Cardiomyrtus that are endemic to the Stirling Range can produce multiple stems from a woody base. A third growth form, with adventitious roots produced from prostrate stems, is found only in H. minus (Strid & Keighery) Keighery.

Stem shape and surface. In cross-section the stems may be circular, 4-angled or 4-winged in sect. Cardiomyrtus, whereas they are 3-angled in sect. Verticilla. The surface is glabrous in sect. Verticilla and four species of sect. Cardiomyrtus but has short, terete, simple hairs in H. phillipsii. Hypocalymma cordifolium has the most prominently winged stems (Figure 2A) in the genus. These wings project from the stem in the same direction as the leaves below and at right angles to the leaves above. Consequently, the wings of each internode are at right angles to the wings of adjacent internodes.

Table 1. Comparison of the sections of *Hypocalymma*. Distribution districts are *Interim Biogeographic Regionalisation for Australia (IBRA) Version 6.1* regions (Department of the Environment, Water, Heritage and the Arts 2008). Rainfall is based on Bureau of Meteorology (2013) data for the last century. 'Peduncle' length includes the length of the secondary axis when present. Degree of unity of the filaments is defined as follows: *basal tube* = united for less than 1/4 of their length; *short tube* = united for *c*. 1/3 of their length; *long tube* = united for at least half of their length. The position of the inner protrusion on the seed is defined as follows: *around hilum* = base of the protrusion extends right around the base of the hilum; *above hilum* = base of the inner protrusion is above the hilum, except for narrow lateral wings.

Character	sect. Cardiomyrtus	sect. Hypocalymma	sect. Verticilla
		excluding <i>H. puniceum</i> group	
distribution			
known districts	ESP, JF, SWA, WAR	AW, ESP, JF, MAL, SWA, WAR	WAR
annual rainfall	600->1,200 mm	300->1,200 mm	>1,200 mm
young stems			
angles	absent or 4	absent or 4	3
ridges	absent or 2	absent, 2 or 4	3
leaves			
arrangement	opposite	opposite	whorled
margins	recurved	usually level or incurved	recurved to revolute
colour	darker above	concolorous or darker below	darker above
venation	brochidodromous	only midvein visible	only midvein visible
oil glands	many and scattered	in several rows	in several rows
inflorescence			
flowers per axil	1–4	mostly 2	1
'peduncle' length	1.5–16 mm	0–2.5 mm	2–4 mm
pedicel length	0-0.8 mm	0–0.8 mm	0.7-1.2 mm
androecium			
filaments	10-50	12–150	15–26
position of long	outermost or	outermost or	alternating with
filaments	nearest to petals	nearest to petals	the short filaments
degree of unity	basal tube	basal or short tube	long tube
staminodes	rare or absent	rare or absent	antipetalous or absent
anther cells	± straight	often curved	straight
connective gland	dorsal	ventral or obscure	dorsal
gynoecium			
ovules per loculus	2 or 6–12	1–11	1 or 8–10
ovary summit	sometimes \pm ridged	often ridged, rarely winged	not ridged
seeds			
length	0.8–1.7 mm	1.3–2.4 mm	1–1.3 mm
testa	smooth or colliculate	pitted	smooth
protrusion	above hilum	around hilum	above hilum

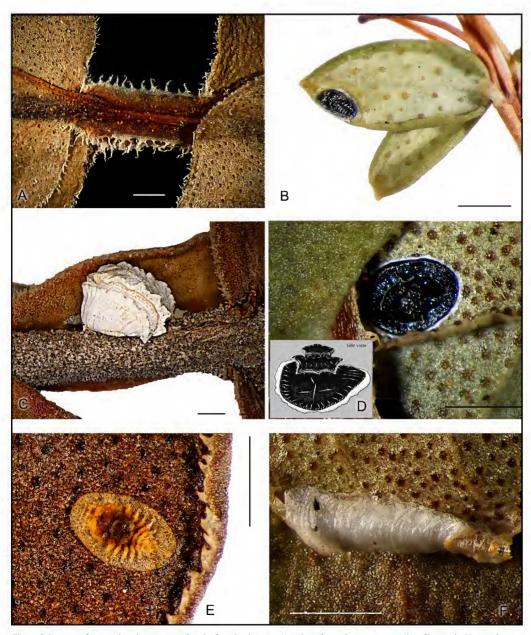


Figure 2. Images of vegetative characters and scale-forming insects. A—winged stem between two pairs of leaves in *Hypocalymma cordifolium*; B—black scale of a white fly larva attached to the pale undersurface (close to the distinctly darker, revolute margin) on a leaf of *H. verticillare*; C—shell-like scale of a female *Callococcus* larva on a hairy stem of *H. xanthopetalum* (sect. *Hypocalymma*); D—image and drawing of a white fly scale, with the empty scales of two previous instars retained on its dorsal surface, attached to a leaf of *H. cordifolium*; E—translucent brown scale, possibly of a coccid, close to a recurved margin on a leaf of *H. cordifolium*; F—diaspid scale on a leaf of *H. cordifolium*. Scale bars are 1 mm. Images taken by Alex Williams from *R.F. Williams s.n.* 16 Sep. 1932 (A, E), *B.L. Rye* 250505 & E.D. Middleton (B), M. Rose 111 (C) and R. Davis 7980 (D, F).

Stem ridges. The 3-angled stems in sect. Verticilla are also 3-ridged, both characters being related to the ternate leaf arrangement in this plant group (Figure 3A). From the base of each petiole, a prominent, rounded, smooth ridge extends down to the next node; the ridge is broadest distally, tapering towards its base. Like the leaves, the three ridges of each internode alternate their orientation with those of the previous internode. Less prominent ridges occur on the stems of some species of sect. Hypocalymma but these may continue down the stem until they reach the top of the next leaf that is orientated in the same direction as the leaf where they began. These species, all with an opposite-decussate arrangement of the leaves, may therefore have a total of four ridges along each internode, even though only two ridges arise at each node. In sect. Cardiomyrtus there are usually no ridges or only 2 slight ridges.

Leaf phyllotaxy. All species of sect. Cardiomyrtus have opposite and decussate leaves, although one specimen (B.L. Rye 290125) from the easternmost population of H. minus has a few stems or portions of stems with leaves in whorls of three in addition to stems with uniformly opposite leaves. Section Verticilla is readily distinguished by its regular arrangement of the leaves in alternating whorls of three, a character found in very few species of the tribe Chamelaucieae. Indeed, uniformly whorled leaves are very rare or absent in all tribes of Myrtaceae in south-western Australia.

Leaf size. Compared with other members of the tribe Chamelaucieae, the taxa described here have medium-sized to very large leaves. *Hypocalymma myrtifolium* Turcz. and *H. phillipsii* have leaves up to 40 mm long and 20 mm wide; in terms of their surface area, these leaves are the largest in the tribe.

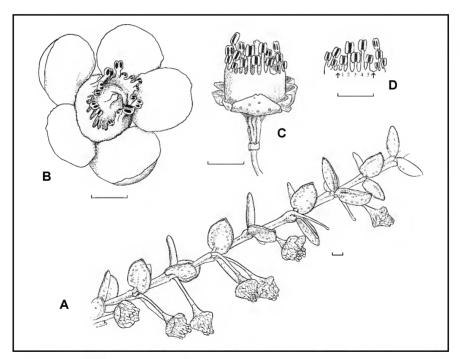


Figure 3. *Hypocalymma verticillare* A – fruiting branchlet, showing ridged stem, whorled leaves and long, curved peduncles; B – flower, showing an immature style and irregular circle of very heterogeneous anthers with bi-coloured thecae; C – fruit, showing a mature style surrounded by filaments united into a long, regular tube; D – part of the androecium from the previously illustrated fruit, with the five anthers opposite the closest sepal numbered and with arrows showing a staminode and a gap (opposite abscised petals). Scale bars are 1 mm. Drawn by Lisa Rye using photographs taken by Peter Rye (A, B) and from *E.D. Middleton* 702 (C, D).

Petioles. Both species of sect. *Verticilla* have short but very well defined petioles. Petioles are short or more commonly absent in sect. *Cardiomyrtus*, with *H. minus* being the only species that is regularly petiolate.

Leaf blades. All species of sect. Cardiomyrtus have broad, thin leaves dotted with very numerous, minute oil glands (see Figure 2E). On each side of a prominent midvein, a faint pattern of venation is often visible, with multiple, parallel secondary veins extending towards the margin and then linking up to form an intramarginal vein. This kind of pinnate venation, known as brochidodromous, was considered by Johnson and Briggs (1984) to be the primitive kind of venation in the Myrtaceae as a whole. Similar venation occurs in the eastern Australian species Sannantha pluriflora (F.Muell.) Peter G.Wilson, but most members of the Chamelaucieae have very reduced leaves that either lack any obvious venation or have only the midvein clearly visible. The upper surface of the leaf in sect. Cardiomyrtus is darker than the undersurface and the margins are recurved.

In leaves of sect. *Verticilla* only the midvein is visible and there are fewer oil glands, which occur mainly in two or three irregular rows on each side of the midvein. As in sect. *Cardiomyrtus*, the upper surface is darker but the margins are more strongly recurved or revolute (Figure 2B).

Inflorescence type. Briggs and Johnson (1979) suggested that the basic inflorescence in *Hypocalymma* is the monad, but noted that the flowers are frequently borne on a brachyblast, a short axillary shoot with only one or two nodes that usually does not grow on. The paired flowers, therefore, constitute what these authors referred to as a conflorescence. This can be observed easily in sect. *Cardiomyrtus* where the flowers are usually in pairs in the axils, borne on a much reduced lateral axis, each one subtended by a single bract. When four flowers occur, the lateral short shoots are conspicuous and can be up to 12 mm long. All flowers have stalks (referred to in the descriptions below as secondary axes) below the bracteoles, although these can be very short in *H. phillipsii* and *H. myrtifolium*. Bracteoles occur at the base of the hypanthium, which is often obtuse but narrows to a distinct anthopodium (also known as a pedicel) in some species, e.g. *H. myrtifolium*. The bracteoles tend to persist longer in this section than in sect. *Verticilla*.

Section *Verticilla* has solitary axillary flowers, which could be interpreted as the plesiomorphic state. There are, therefore, a maximum of three flowers per node arranged in alternating whorls of three, although some nodes have one or two barren axils and are therefore only 1- or 2-flowered. Once pressed, flowering branchlets often appear to have all the flowers to one side rather than evenly arranged on the stem because the peduncles are fairly long and curve downwards so that the flowers are somewhat pendulous. The pedicels are distinctly shorter than the peduncles. The bracteoles are narrow and scarious, and are apparently either caducous or deciduous.

Calyx and corolla. Sepals are well developed in all species of Hypocalymma, although much shorter than the petals. In sections Cardiomyrtus and Verticilla the sepals are obtuse, with a petaline margin and with the midrib herbaceous but not prominently ridged. The latter section has shortly but narrowly clawed, white petals, which are widely spreading in flower and deciduous in fruit. In sect. Cardiomyrtus, four species are white-flowered but one has deep pink petals, and the petals of three of the species are persistent in fruit.

Stamen number and degree of fusion. In all species of Hypocalymma the stamens are of a varied rather than a fixed number in each flower. Most members of sections Hypocalymma and Cardiomyrtus have stamens arranged in two or three series and shortly united at the base into a complete circle. However,

H. minus of sect. *Cardiomyrtus* has the lowest numbers of stamens in the genus, down to ten per flower, with all or most filaments free, and has no stamens opposite the petals. In sect. *Verticilla* the filaments are broader than those of sections *Hypocalymma* and *Cardiomyrtus* and they are united for about half their length. The height of the united part of the androecial ring is more or less uniform around the circle (see Figure 3C).

Reduced stamens and staminodes. Unlike all other species of Hypocalymma, H. verticillare (sect. Verticilla) commonly has staminodes. Its stamens appear to form five antisepalous groups because the free parts of the filaments differ greatly in size (Figure 3B–D). There is usually a solitary staminode or a very small stamen (with a very small anther) directly opposite each petal, although this may sometimes be replaced by a small gap (see Figure 3D), and there are two to five stamens opposite each sepal. The longest stamens have a large anther and always occur adjacent to shorter stamens with a smaller anther. Although the other species of sect. Verticilla, H. connata, lacks staminodes and has little variation in anther size, it is similar to H. verticillare in having long and short filaments alternating.

Anthers. Anthers in sections Cardiomyrtus and Verticilla are basifixed or almost basifixed. They have a free connective gland and well defined, longitudinally dehiscent thecae, which are usually straight and parallel. The connective tends to be broader and the thecae shorter and more strictly introrse in sect. Verticilla than in sect. Cardiomyrtus. The connective gland is most obvious in young anthers. Once the anthers have dehisced, the connective gland may be difficult to see in sect. Cardiomyrtus although it is always obvious in H. minus and in sect. Verticilla. The latter section has the thecae strongly bi-coloured (Figure 3B) with the pale outside rim very clearly distinguished from the central reddish area of dehiscence.

Pollen. Longicolpate pollen has been recorded in two sections of Hypocalymma. Two species of sect. Hypocalymma, H. robustum (Pike 1956: Figure 82) and H. angustifolium (Patel et al. 1984: Figure 44E, G), have a patterned surface, straight sides (rather than convex or concave) and very long colpi reaching to near the centre of the grain but not meeting. Pollen of similar size and other characteristics was recorded but not illustrated (Pike 1956) for H. phillipsii of sect. Cardiomyrtus. Thornhill et al. (2012) adopted a somewhat different terminology for colpal morphology, using the term 'brevicolpate' in place of 'longicolpate'. Their results generally confirmed the published observations cited above except that they also recorded pollen with convex and concave sides, and there was variation in the colpal morphology of H. xanthopetalum of sect. 'Chrysocalymna', including both acolpate and syncolpate forms. The question of whether or not such variation in pollen morphology has phylogenetic value must await a more comprehensive study of pollen variation in the genus.

Gynoecium. In sect. Hypocalymma the ovary is 2- or 3-locular and its summit is often prominently ridged along the centre of each loculus where the line of dehiscence is located. Many species completely lack a depression for the style, instead having the style base thick and continuous with the raised intersection of the ridges at the centre of the ovary summit, while other species have the style base inserted in a shallow or deep depression. Sections Cardiomyrtus and Verticilla have a 3-locular ovary with the summit 3-lobed but not or scarcely ridged, and the style is always in a depression that reaches down to the level of the placentas.

Fruits. The capsule of sect. *Verticilla* is half-inferior to two-thirds-superior, with the superior part closely surrounded by the persistent, connate part of the androecium. In sect. *Cardiomyrtus* the capsule is half-inferior to almost fully superior and the stamens tend to be shed before the fruit matures unless they are retained within persistent closed petals.

Seeds. The seeds of sect. Hypocalymma (Figure 4A) are 1.3–2.4 mm long and have an irregularly ovoid, shallowly to very deeply pitted, brown body containing the seed and a prominent swelling extending from the top of the inner surface down most of the length of the seed but not reaching the base. This inner protrusion is concentrated above the hilum but often also narrowly encircles the base of the hilum. In sections Cardiomyrtus (Figure 4B) and Verticilla (Figure 4C, D) the seeds are of a similar shape to those of sect. Hypocalymma but they are smaller (0.8–1.7 mm long) on average and the inner protrusion does not extend around the base to the hilum. The testa is colliculate in H. speciosum and smooth in the other six species.

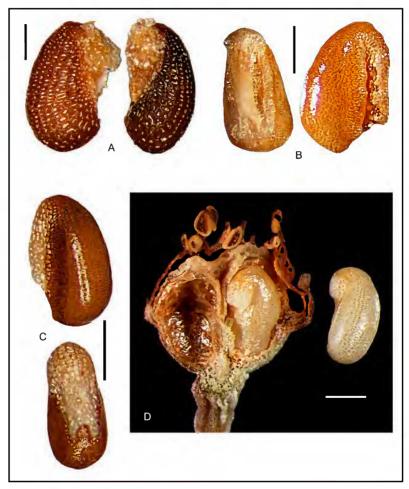


Figure 4. Images of seeds. A – lateral view of pitted seeds of the sect. *Hypocalymma* species *H. elongatum* (Strid & Keighery) Rye; B – inside and lateral views of smooth seeds of *H. myrtifolium*; C – inside and lateral views of smooth seeds of *H. connatum*; D – lateral view of smooth seeds of *H. verticillare*, with one *in situ* in a fruit. Scale bars are 0.5 mm. Images taken by Alex Williams from *J.M. Powell* 3276 & *M. Hardie* (A), A.S. George 3124 (B), C.A. Gardner s.n. Sep. 1935 (C) and B.L. Rye 250504 & E.D. Middleton (D).

Chaff. In the species with 8–12 ovules per loculus, some ovules in each loculus usually fail to develop into a fertile seed. These chaff pieces are reduced in size but mostly still have a crustaceous testa. In *H. cordifolium* and *H. minus*, which have two ovules per loculus, a highly compressed, membranous chaff piece is produced in loculi that have a single seed. As there is only one ovule per loculus in *H. verticillare*, there is no possibility of chaff being produced in the same loculi as seeds.

Habitat

Most members of the tribe Chamelaucieae occur in regions with less than 600 mm annual rainfall. *Hypocalymma* sections *Cardiomyrtus* and *Verticilla* are restricted to parts of the far south-west of Western Australia (Figure 5) where the annual rainfall varies from about 600 to over 1,200 mm (see Table 1). The relatively high humidity of their environment is reflected in some aspects of their morphology. For example, the very broad, stem-clasping leaves of *H. cordifolium* (sect. *Cardiomyrtus*) often form a more or less complete circle of green at each node, similar in effect to the whorled leaves in sect. *Verticilla* in terms of providing a large surface area for photosynthesis.

Section *Hypocalymma* is much more speciose and widespread than the two other sections and has its greatest development in the northern sandplains, although it is still entirely restricted to the South West Botanical Province of Western Australia. Within the genus as a whole, there is a tendency for larger seeds with a thicker testa to occur in species from the northern sandplains and central wheatbelt than in species from the areas of higher rainfall in the south. The smallest seeds occur in members of sections *Cardiomyrtus* and *Verticilla* that are associated with swamps or watercourses in the far south-west.

Section *Verticilla* seems to be a relictual group, close to extinction. One of its two species may already be extinct and the other is known only from a single population. Presumably this group evolved during a period of higher rainfall than is currently found in south-western Australia, radiated to a significant degree, as evidenced by the many differences between the two known species, and then declined. Hopper and Gioia (2004: 636) noted that waterlogged or moisture-retaining soils in the south-west 'provide habitat for the phylogenetically relictual taxa of the region' with most of these taxa occurring in the high rainfall zones of the extreme south-west or eastwards along the south coast. *Hypocalymma* sect. *Verticilla* appears to fit this trend well.

Phenology and breeding systems

The new species *H. verticillare* has an unusual autumn flowering period from March to May, a factor that may have delayed its discovery. The other species included in this revision tend to flower primarily in spring or summer, mainly from September to December, although two of them have been recorded in flower throughout the year.

The breeding systems of four species of *Hypocalymma* sect. *Cardiomyrtus* (*H. cordifolium*, *H. minus*, *H. myrtifolium* and *H. speciosum*) have been studied by one of us (GJK) in cultivation at Kings Park. All species had flowers adapted to outcrossing and did not set seed when manually self-pollinated.

Insect associations

Solitary native bees, mostly *Leioproctus* species, have been recorded visiting *Hypocalymma* flowers, as has the European Honey-bee, *Apis mellifera* (Houston 2000). Other insect visitors may also play a role in pollination and there are also limited records of honeyeaters and the Honey Possum, *Tarsipes rostratus*, visiting *Hypocalymma* species (Brown *et al.* 1997).

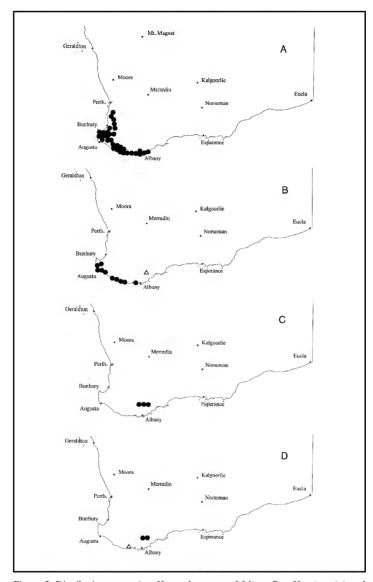


Figure 5. Distribution maps. A – Hypocalymma cordifolium; B – H. minus (\bullet) and H. myrtifolium (\triangle) ; C – H. phillipsii; D – H. speciosum (\bullet) and H. verticillare (\triangle) .

Granivorous insects

Granivorous bugs belonging to the family Lygaeidae seem to be particularly diverse and abundant in the seed litter under *Hypocalymma* species (Slater 1975, 1976), often forming large populations and with several species from varied genera sometimes found under a single shrub. They are also common under a number of legume and epacrid genera that have myrmecochorous seeds. Main (1981) suggested that the development of highly evolved elaiosomes leading to the removal of seeds by ants in such genera may have evolved as an effective defence against seed predation by lygaeid bugs. This could be the primary selection pressure for myrmecochory within Chamelaucieae.

Although Berg (1975) lists no Myrtaceae as myrmecochorous, the presence of a fleshy aril on *Rinzia* (Trudgen 1986: Figure 2), *Ochrosperma* Trudgen and *Euryomyrtus* Schauer indicates that these genera are very likely to have ant-dispersed seeds. We are currently unsure how important ants are in the dispersal of *Hypocalymma* seeds and whether the seeds have a genuine reward for ants or just mimic the myrmecochorous seeds of genera with true elaiosomes (see Rye & Trudgen 2008). However, we do have direct evidence of myrmecochory in *Hypocalymma*. During the summer of 1986, one of us (GJK) observed workers of the ant species *Iridomyrmex purpureus* collecting fallen seeds of *H. myrtifolium* on Bluff Knoll. Ants have also been observed collecting seeds of *H. ericifolium* Benth. at Harvey.

Scale-forming insects

Hypocalymma sect. Cardiomyrtus is host to many kinds of scale-forming insects that feed on sap, and these are most prevalent in H. cordifolium. The stems of H. cordifolium are commonly infested by the felt-scale genus Callococcus (Hemiptera family Eriococcidae). Male larvae produce small, felt-like covers at the nodes, while female larvae produce large, shell-like scales. Callococcus scales also occur commonly on species belonging to sect. Hypocalymma (Figure 2C) and on the two most closely related genera Astartea (Rye 2013: Figure 6A, B) and Cyathostemon but are unknown in any other members of the tribe Chamelaucieae.

Several other kinds of scales observed on *H. cordifolium* occur on the leaves. Many are produced by white fly larvae (Hemiptera family Aleyrodidae), whose scales can be identified by the sculpturing of their surfaces, with lines, grooves and pits, and often also by the appearance of their waxy borders. One kind that is commonly observed on the undersurface of leaves is black with a narrow, shiny, white border. It is dorsiventrally very compressed and increases in size as the larva progresses through several stages (instars). The most mature scale commonly retains the empty scale of the previous instar, or even two previous instars (Figure 2D), on its dorsal surface. For convenience this structure is referred to here as a compound scale. It is also known on *H. phillipsii* but has not been found to date on any species of sections *Hypocalymma* and *Verticilla*, nor on any other members of the tribe, suggesting that it may be specific to sect. *Cardiomyrtus*.

Another kind of black scale, observed on only one specimen (*J. Dewing* 922) of *H. cordifolium* and also one specimen (*G.J. Keighery* 6192) of *H. myrtifolium*, seems to match the white fly scales that are common in *H. verticillare* of sect. *Verticilla* (Figure 2B). These scales are simple (i.e. the scales of previous instars are shed not retained) and tend to be smaller than the compound kind that is commonly found on *H. cordifolium*. They also differ in their location, occurring always near the edge of the leaf where they tend to be partially hidden by the recurved margin.

A much rarer scale, observed on only two specimens (e.g. *R.F. Williams s.n.* 16 Sep. 1932) of *H. cordifolium*, is pale brown with the body of the larva visible through the translucent scale (Figure 2E) and appears to be a coccid (Hemiptera family Coccidae). No other members of the tribe Chamelaucieae are known to have this kind of scale, but it is not as obvious as the black scales and would be more readily overlooked.

Another insect group (Hemiptera family Diaspidae) observed in *H. cordifolium* has a scale shaped more like a long tear drop, with the narrowed end pale brown and the rest white (Figure 2F). This diaspid is also known on *H. myrtifolium* but its occurrence on other members of the genus has not been investigated.

Taxonomic relevance

The conspicuous, stem-attached *Callococcus* scales have been recorded on each of the three genera that constitute the *Astartea-Cyathostemon-Hypocalymma* clade of Wilson *et al.* (2004) but not on any other genera of Chamelaucieae, providing independent support for the clade. Some white flies are also highly host-specific (Woodward *et al.* 1970: 418), and the apparent restriction of the compound scale type to sect. *Cardiomyrtus* may provide additional evidence for the distinctiveness of this section. Other kinds of insects may also be significant, but a complete survey of their occurrence throughout the tribe Chamelaucieae is needed to determine whether or not they are of any value in suggesting taxonomic relationships between groups of taxa or in defining individual groups.

Taxonomy

Key to species with smooth or colliculate seeds

1. Young stems 3-angled, each angle with a rounded ridge that extends down from the base of the petiole above. Leaves in whorls of three, with oil glands in 2 or 3 main, irregular rows on each side of the midvein. Flowers solitary in the axils. Androecium of 15–26 filaments, united for at least half of their length (<i>Hypocalymma</i> sect. <i>Verticilla</i>)		
2. Leaf blades $c. 7 \times 1-1.5$ mm. Petals 3.5–4 mm long, persistent in fruit. Anthers all of a similar size. Ovules multiple in each loculus (distribution unknown)		
2: Leaf blades 3–6 × 1.8–2.3 mm. Petals 2–2.5 mm long, deciduous. Anthers very variable in size. Ovules solitary in each loculus (N of Walpole)		
1: Young stems all or mostly ± terete to 4-winged, the 4 angles or wings (when present) not aligned with the petioles. Leaves all or mostly opposite, dotted with numerous minute oil glands. Flowers up to 4 per axil, rarely all solitary. Androecium of 10–50 filaments, shortly united at the base or free (<i>Hypocalymma</i> sect. <i>Cardiomyrtus</i>)		
3. Leaves ovate to obovate to broadly elliptic, 15–40 mm long. Ovules horizontal, 6–12 per loculus. Seeds with hilum near base of inner surface		
4. Young stems and peduncles with minute hairs. Petals 6–9 mm long (Stirling Ra.) H. phi		
4: Young stems and peduncles glabrous. Petals 4.5–6.5 mm long (eastern Stirling Ra.) H. myrtifolium		
3: Leaves cordate or very broadly ovate to almost circular, 4–19 mm long. Ovules erect, 2 per loculus. Seeds with hilum near centre of inner surface.		
5. Petals deep pink-purple, 6–7 mm long. Ovary superior in flower. Seeds 1.6–1.7 mm long, minutely but distinctly colliculate (Stirling Ra.)		
5: Petals white or pale pink, 1.2–4.5 mm long. Ovary about half-inferior in flower. Seeds 0.8–1.3 mm long, smooth.		
6. Leaves cordate or depressed cordate, 6–19 mm long. Petals 2.5–4.5 mm long. Stamens 25–40, opposite petals as well as sepals. Mature style 2.5–5 mm long (Jarrahdale–Margaret River area–Cape Riche)		
6: Leaves ovate to cordate, 4–8(–10) mm long. Petals 1.2–2 mm long.		

Stamens 10–20, opposite sepals but not petals. Mature style 0.6–1.2 mm long

Hypocalymma sect. **Cardiomyrtus** Schauer, in J.G.C. Lehmann, *Pl. Preiss.* 1: 112 (1844). *Type: Hypocalymma cordifolium* Lehm. ex Schauer.

Hypocalymma sect. Calocalymna Turcz., Bull. Soc. Bull. Soc. Imp. Nat. Moscou 35(4): 325–326 (1862), nom. inval. Type: Hypocalymma speciosum Turcz.

Shrubs 0.1–1(-1.5) m high, commonly with multiple suberect stems from a woody base or with adventitious roots produced from prostrate stems. Young stems glabrous or with minute simple hairs, 4-angled (very rarely 3-angled in H. minus) or irregularly terete, sometimes with the angles slightly to very prominently winged. Leaves opposite and decussate (very rarely in whorls of 3 in H. minus). Petioles absent or short. Leaf blades elliptic to cordate, thin, with recurved margins, dotted with numerous minute oil glands, discolorous, the pale green undersurface with more obvious oil glands than the much darker upper surface, glabrous throughout or with margins laciniate to ciliate. Inflorescence with 1-4 flowers per axil, most axils 2-flowered in most species but 1-flowered in H. minus. Peduncles up to 11 mm long but sometimes ± absent. Secondary axes (when present) up to 12 mm long. Bracteoles 2 per flower, broader and often longer than the bracts. Pedicels short or absent. Hypanthium shortly cup-shaped or more obconic, usually rugose. Sepals well developed but much shorter than petals, broad-based, obtuse, largely herbaceous but with a narrow petaline border. Petals 1.2-9 mm long, white to deep pink, narrowed or shortly clawed at base. Staminodes rare or absent. Stamens (10–)13–50, in 2 series forming a complete ring (but one series sometimes with few stamens) when numerous but all antisepalous when few (i.e. 10-20), the longest stamens in the outer series when numerous or those closest to the petals when few, united shortly at base or free. Ovary 3-locular, half- to fully superior, the superior part with 3 rounded lobes, not or scarcely ridged; ovules 2 or 6-12 per loculus. Style with base inset into a cylindrical depression in the summit of the ovary; stigma small, capitate or slightly peltate. Fruits thick-walled. Seeds crustaceous, usually \pm ovoid to reniform; body unfacetted or somewhat facetted, whitish to medium brown, smooth or minutely colliculate, 0.8-1.7 mm long; inner protrusion large, forming a distinctly coloured zone on inner surface of seed distal to the hilum, usually also extending laterally along each side of hilum but not fully encircling it; hilum small, sub-basal to central. Chaff pieces much smaller than seeds.

Size and distribution. A group of five species, restricted to the extreme south-west of Western Australia, with three species occurring in the Stirling Range and the others extending from Jarrahdale south to Augusta and along the south coast east to Cape Riche.

Etymology. From the Greek kardia (heart) and the genus Myrtus L., referring to the heart-shaped leaves in this myrtaceous group. Heart-shaped leaves are rare in Chamelaucieae but occur in three of the five species of Hypocalymma sect. Cardiomyrtus, including the type species H. cordifolium.

Affinities. See notes under H. sect. Verticilla.

Notes. Hypocalymma sect. Cardiomyrtus is reinstated here. It is a relatively well known plant group, with at least four of its five species in cultivation by 1990 and with *H. cordifolium* also used in the cut-flower trade (Elliot & Jones 1990). Within the key to *Hypocalymma* in Blackall and Grieve (1980: 91), the four species of *H.* sect. Cardiomyrtus that had been named by that stage are accurately keyed and illustrated.

Very little fruiting material is available for the three species from the Stirling Range but they all appear to have crustaceous chaff pieces of a similar colour to, or paler than, the seeds.

Hypocalymma cordifolium Lehm. ex Schauer, in J.G.C. Lehmann, *Pl. Preiss*. 1: 112 (1844). *Hypocalymma cordifolium* Schauer subsp. *cordifolium* in Strid & Keighery, *Nord. J. Bot*. 22: 565 (2002). *Type*: Albany, Western Australia, October 1840, *L. Preiss* 154 (*lecto*: LD, *fide* A. Strid & G.J. Keighery, *Nord. J. Bot*. 22: 565 (2002); *isolecto*: K, KW, MEL, S, W).

Illustrations. W.E. Blackall & B.J. Grieve, *How Know W. Austral. Wildflowers* 3A: 91, n. 9 (1980); J.R. Wheeler, N.G. Marchant & M. Lewington, *Fl. South West* 2: 707 (2002).

Shrub up to 1 m high, single-stemmed at base where known. Young stems prominently 4-winged, sometimes becoming deep red; wings patent, extending the length of each internode, tending to be broadest at the apex and extending laterally from the petioles or leaf base directly above, alternating in direction at successive internodes in a decussate arrangement, commonly 0.5–1.2 mm wide, often ciliate to laciniate. Petioles absent or up to c. 0.5 mm long. Leaf blades mostly patent, cordate, 6–19 mm long, 9–18 mm wide, acute or obtuse, often distinctly ciliate; apical point absent or poorly defined, up to 0.3 mm long; midrib indented on upper surface and prominent on lower surface. Inflorescence occupying 1-16 nodes per branchlet. Peduncles 1-4-flowered, up to 11 mm long if 1-flowered, up to c. 5 mm long but with long secondary axes if multi-flowered. Secondary axes 4-11 mm long. Bracteoles deciduous or persistent, linear or narrowly obovate, 1.3–2 mm long, green or red-tinged. Pedicels absent or up to 1.3 mm long. Flowers 7-11 mm diam. Hypanthium strongly rugose-pitted or smoother but glandular. Sepals broadly oblong-elliptic to depressed ovate, 1.5–2 mm long, 1.9–2.3 mm wide, the herbaceous part green or red-tinged; petaline margin c. 0.3 mm wide, usually white and tinged deep pink. Petals 2.5-4.5 mm long, white or pale pink, deciduous. Stamens 25-45, united at base in a full circle opposite petals as well as sepals. Longest filaments 2-4 mm long, united for up to 0.5 mm at base. Anthers 0.2–0.3 mm long. Ovary c. half-inferior; ovules 2 per loculus, erect. Style 2.5–5 mm long. Fruits at least half-superior, 1.5–1.7 mm long. Seeds 1.1–1.3 mm long, 0.5–0.6 mm wide, 0.6–0.7 mm deep, off-white (pearly) or pale brown, smooth; inner protrusion 0.4–0.6 mm long, 0.2–0.5 mm deep, white or off-white; hilum at centre of inner surface. Chaff pieces membranous, very compressed, darker than the seeds. (Figure 2A)

Selected specimens examined. WESTERN AUSTRALIA: Samson Brook transect, 26 Sep. 2000, *R.R. Archer* 124 (PERTH); 30 km NNE of Albany, between Bettys Beach and NE side of Two Peoples Bay, 26 Sep. 2004, *R.K. Brummitt, A.S. George & E.G.H. Oliver* 21358 (PERTH); 14.2 km E of Sues Rd on Crouch Rd, 21 Nov. 2008, *G.J. & B.J. Keighery* 1422 (PERTH); 500 m W of corner of Swarbrick and Osmington Rds, E of Margaret River, 23 Aug. 2007, *M. Morley* 115 (PERTH); W end Lake Powell Nature Reserve, *c.* 100 m S of end of Hassell Rd, 20 Nov. 2007, *E.M. Sandiford & D.A. Rathbone* 1386 (PERTH).

Distribution and habitat. Extends from Jarrahdale south to near Margaret River and along the south coast east to Cape Riche (Figure 5A), in damp habitats, mainly associated with swamps or watercourses.

Phenology. Flowers all year but mainly September to November. Fruits mainly recorded November to January.

Conservation status. Not considered to be at risk. This species is widely cultivated as well as being the most widespread species in its section.

Affinities. Very similar to H. minus, as discussed under that species.

Notes. Hypocalymma cordifolium is the most variable species in sect. *Cardiomyrtus*. Cultivars of *H. cordatum* include one with variegated leaves. Flower size in natural populations is very variable, with the smallest flowers of a similar size to the largest flowers found in *H. minus*. Anther morphology is also variable, and sometimes the thecae become latrorse and curved rather than being straight and parallel.

Hypocalymma cordifolium may be a particularly important host plant for Hemipterous species that feed on sap (see *Insect associations* section above). Seed-eating bugs belonging to the genera *Botocudo* and *Isopeltis* (Hemiptera family Lygaeidae) have been recorded in its seed litter (Slater 1975).

Several of the specimens cited for this taxon by Strid and Keighery (2002), as subsp. *cordifolium*, have now been re-identified as *H. minus*. These are cited below.

Hypocalymma minus (Strid & Keighery) Keighery, stat. et comb. nov.

Hypocalymma cordifolium subsp. minus Strid & Keighery, Nord. J. Bot. 22: 567–568 (2002). Type: by Brennans Ford, Scott River Crossing, east-north-east of Augusta, Western Australia, 16 November 1982, A. Strid 21416 (holo: C; iso: B, G, MEL, MO, PERTH 1175823 & 1945165).

Hypocalymma sp. Scott River (A.S. George 11773), Western Australian Herbarium, in FloraBase, http://florabase.dec.wa.gov.au [accessed March 2013]; G. Paczkowska & A.R. Chapman, West. Austral. Fl.: Descr. Cat. 387 (2000); J.R. Wheeler, N.G. Marchant & M. Lewington, Fl. South West 2, 708 (2002).

Illustration. J.R. Wheeler, N.G. Marchant & M. Lewington, *Fl. South West* 2: 708 (2002) as *Hypocalymma* sp. Scott River (A.S. George 11773).

Shrub usually 0.1–0.4 m high, almost prostrate or low-growing, sometimes layering from decumbent or prostrate stems. Young stems slightly to prominently 4-winged (rarely with some stems 6-winged); wings patent, extending the length of each internode, tending to be broadest at the apex and extending laterally from the petioles or leaf base directly above, alternating in direction at successive internodes in a decussate arrangement, commonly 0.2–0.5 mm wide, sometimes ciliate. Petioles 0.1–0.5 mm long. Leaf blades mostly patent, ovate to cordate, rarely all cordate, 4–8(-10) mm long, 3–9 mm wide, acute or obtuse, often distinctly ciliate; apical point up to 0.3 mm long, white. *Inflorescence* occupying 1 to many nodes per branchlet. Peduncles 1-flowered, 4-11 mm long. Bracteoles deciduous or persistent, narrowly ovate to \pm narrowly elliptic or ovate, 0.7–1.5 mm long, rather scarious, green or red-tinged. Pedicels absent. Flowers commonly 4-6 mm diam. Hypanthium rugose or glandular. Sepals very broadly or depressed ovate to almost semicircular, 0.6-1.3 mm long, 1-1.6 mm wide, the herbaceous part green or red-tinged; petaline margin c. 0.3 mm wide, white or tinged deep pink. Petals 1.2-2 mm long, white, deciduous. Stamens 10–20, opposite sepals but not petals, all or mostly free. Longest filaments 0.5–1 mm long, free or united for up to 0.2 mm at base. Anthers 0.2–0.3 mm long. Ovary c. half-inferior; ovules 2 per loculus, erect. Style 0.6–1.2 mm long. Fruits at least half-superior, 1.3–1.5 mm long. Seeds 0.8–1.1 mm long, c. 0.5 mm wide, c. 0.6 mm deep, off-white (pearly) or pale brown, smooth; inner protrusion 0.4–0.5 mm long, c. 0.2 mm deep, white or off-white; hilum at centre of inner surface. Chaff pieces membranous, very compressed, darker than the seeds.

Selected specimens examined. WESTERN AUSTRALIA: Sandy Track, D'Entrecasteaux National Park, 23 Dec. 2002, R.J. Cranfield 18736 & L. Sage (PERTH); Black Point, D'Entrecasteaux National Park, 31 Oct. 1990, N. Gibson & M. Lyons 989 (PERTH); 14.2 km E of Sues Rd on Crouch Rd, 21 Nov. 2008, G.J. & B.J. Keighery 1423 (PERTH); 600 m S along track from Chesapeake Rd, 3 Nov.

2009, *J. Liddelow* 107 (PERTH); Augusta townsite, 8 June 1989, *G. McCutcheon* 2078 (PERTH); on walking track down to the beach from the car park at the end of Crusoe Beach Rd, Rudgyard Nature Reserve, 6 Jan. 2010, *B.L. Rye* 290125 (PERTH); *c.* 200 m NW of Railway Parade, W of Walpole, 25 Apr. 2008, *M. Sowry* 109 (PERTH).

Distribution and habitat. Occurs in the extreme south-west corner of the State and extends along the south coast east to the Denmark area (Figure 5B) in winter-wet to damp, often skeletal loams over an impeding layer, often under a *Taxandria linearifolia* shrubland.

Phenology. Flowers and fruits all year.

Conservation status. This species is not considered to be at risk as it has a range c. 250 km long and is known from many localities, including populations that are protected within national parks and other reserves.

Affinities. Previously treated as a subspecies of *H. cordifolium* but distinguished by its normally prostrate habit, slender stems, smaller leaves, smaller flowers and fewer stamens.

During a survey of plant communities on the Blackwood Plateau in 2008 by one of the current authors (GJK) and Bronwen Keighery, a large co-occurrence of the two subspecies of *H. cordifolium* was located. This locality showed ecological separation of the two taxa, subsp. *minus* (G.J. Keighery & B.J. Keighery 1421) occurring mainly on shallow, winter-wet, red, clay loams over ironstone and subsp. *cordifolium* (G.J. Keighery & B.J. Keighery 1422) on deeper soils along the adjacent creek. However, numerous plants grew side by side within this area and, despite careful searching, no signs of intergradation or hybridisation were detected. This strongly suggested that these were two species, not subspecies; consequently subsp. *minus* is here raised to specific status.

Notes. There is some tendency for the leaves to be ovate on young plants and become more cordate as the plant matures, but some mature specimens retain ovate leaves and some specimens may have even the young leaves cordate.

Hypocalymma myrtifolium Turcz., *Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersburg* 10: 333 (1852). *Type*: 'Nova Hollandia' [Stirling Range, Western Australia], 1848, *J. Drummond* 5: 118 (*holo*: KW 001001304; *iso*: BM, G, K 000797335, 000797331–3, MEL, NSW 456459, PERTH 01637207, W).

Hypocalymma hypericifolium Benth., *Fl. Austral.* 3: 95 (1867). *Type*: Swan River Colony [Stirling Range, Western Australia], 1848, *J. Drummond* 5: 118 (*lecto*: K 000797335, here selected; *isolecto*: BM, G, K 000797331–3, KW 001001304, MEL, NSW 456459, PERTH 01637207, W).

Illustration. W.E. Blackall & B.J. Grieve, How Know W. Austral. Wildflowers 3A: 91, n. 12 (1980).

Shrub 0.3–0.8 m high, often multi-stemmed from a woody base or lignotuber. Young stems glabrous, 4-angled and often somewhat winged; wings up to 0.4 mm wide, sometimes serrulate. Petioles absent. Leaf blades antrorse or patent, ovate to obovate or broadly elliptic (usually ± elliptic), 15–40 mm long, 6–16 mm wide, acute or obtuse, serrulate, sometimes with an apical point up to 0.4 mm long; midrib indented on upper surface and prominent on lower surface. Inflorescence occupying 1–10 nodes per branchlet. Peduncles very reduced, mostly 2-flowered. Secondary axes 1–2.5 mm long. Bracteoles fairly persistent, very broadly or depressed ovate, 1.5–2.3 mm long, obtuse, green or red-

tinged. *Pedicels* absent or very reduced. *Flowers* 13–15 mm diam. *Hypanthium* glandular and rugosepitted, green. *Sepals* very broadly ovate to elliptic, 2–3.5 mm long, 1.8–2.8 mm wide, the herbaceous part usually green; petaline margin 0.3–0.4 mm wide, white or red-tinged. *Petals* 4.5–6.5 mm long, white, persistent. *Stamens* 30–50 in 2 series forming a complete circle. *Longest filaments* 3.5–4.5 mm long, united for *c*. 0.6 mm at base. *Anthers* 0.4–0.7 mm long. *Ovary c*. half-inferior; ovules 6–10 per loculus, horizontal. *Style* 3–4 mm long. *Fruits* over half-superior, *c*. 3 mm long. *Seeds* 1.3–1.4 mm long, 0.5–0.6 mm wide, 0.8–0.9 mm deep including inner protrusion, pale brown or becoming medium brown, smooth; inner protrusion 0.8–1 mm long, 0.2–0.3 mm deep; hilum towards base of inner surface. *Chaff pieces* crustaceous. (Figure 4B)

Selected specimen examined. WESTERN AUSTRALIA [locality withheld for conservation reasons]: 31 Oct. 1994, A. Worz 04.10.31.01 (PERTH).

Distribution and habitat. Restricted to the eastern peaks of the Stirling Range (Figure 5B), on lower rocky slopes to near the summits of mountains.

Phenology. Flowers July to November. Seeds were present on specimens collected in October and November, but these were possibly not fully mature in their colour.

Conservation status. Recently listed as Priority Two under the Department of Environment and Conservation (DEC) Conservation Codes for Western Australian Flora (Western Australian Herbarium 1998–) [now the Department of Parks and Wildlife]. No collections have been made of *H. myrtifolium* since 1994. All populations occur in a large national park but the known range of the species is only about 10 km long. Many plant species from this park, although protected from clearing, are still highly threatened if they are susceptible to attack by the water mould *Phytophthora*. The susceptibility of species of sect. *Cardiomyrtus* to this pathogen is unknown.

Affinities. Very similar to *H. phillipsii*, differing mainly in the absence of hairs on the stems and peduncles and in its usually smaller flowers. *Hypocalymma myrtifolium* also tends to have narrower sepals and its leaves show a greater tendency to be obovate, acute and less prominently pointed than in *H. phillipsii* but there are no absolute differences in these characters. The two taxa are geographically separated, with *H. phillipsii* extending from the western peaks to the south-eastern peaks of the Stirling Range but absent from the north-eastern peaks where *H. myrtifolium* is found.

A comparison of *H. phillipsii* and *H. myrtifolium* using molecular data would be useful to examine how closely related they are, as it is possible they should be regarded as subspecies rather than species. More fruiting material is also needed to determine whether differences observed in the few seed samples examined of the two taxa are significant. The single specimen with seeds from *H. phillipsii* differed from two seeding specimens of *H. myrtifolium* in having darker seeds with a thicker inner protrusion.

Typification. There are four Drummond sheets at Kew, one stamped 'Herbarium Benthamianum 1854', two stamped 'Herbarium Hookerianum 1867', and one ex herb. W.W. Saunders with a sticker saying it was 'Presented by the Linnean Society, 1915'. All sheets have ample flowering material and are annotated in the same hand. There is no certainty that Bentham had only one of these available to him when he drew up his descriptions for *Flora Australiensis*. We therefore consider it necessary to choose a lectotype for *H. hypericifolium* and have selected the specimen indicated as ex Herbarium Benthamianum since it has clear links to Bentham and already bears relatively recent Kew type labels.

Notes. This was one of two Stirling Range species of *Hypocalymma* collected originally by James Drummond, who described them in a letter dated 29 October 1848. He recorded the species now known as *H. myrtifolium* as growing in the woods at the eastern end of one of the mountains of the Stirling Range and stated 'a faithful drawing of which, leaves, flowers and branches might very well pass for the broad leaved Indian Myrtle' (Drummond 1839–1848).

Hypocalymma phillipsii Harv., *Nat. Hist. Rev.* 5(2): 296, t. 22 (1858). *Type*: cultivated in Botanic Garden of Dublin from seeds collected in neighbourhood of King George Sound, Western Australia (*holo*: TCD; *iso*: MEL 104609).

Illustrations. W.H. Harvey, loc. cit. (1858); W.E. Blackall & B.J. Grieve, How Know W. Austral. Wildflowers 3A: 91, n. 11 (1980).

Shrub commonly 0.4–1 m high but recorded up to 1.5 m, erect or sprawling, up to at least 1.5 m across, often producing multiple erect stems from a lignotuber. Young stems somewhat 4-angled or slightly 4-winged to elliptic in cross-section or terete, with a very dense indumentum; hairs patent, up to 0.4 mm long, white or pale brown, obtuse. Petioles absent. Leaf blades mostly antrorse but some (especially those subtending flowers) patent, elliptic to very broadly ovate, 15–40 mm long, 8–20 mm wide, usually obtuse, serrulate, rarely with an apical point 0.3-0.5 mm long; midrib indented on upper surface and prominent on lower surface. Inflorescence occupying 1-4 or rarely up to 9 nodes per branchlet. Peduncles absent or very reduced, up to c. 1 mm long, mostly 2-flowered. Secondary axes 1–7 mm long, with a moderately dense indumentum of simple, patent hairs up to 0.2 mm long. Bracteoles persistent, broadly or very broadly ovate, 1.5-3 mm long, obtuse. Pedicels absent or very reduced. Flowers mostly 14-18 mm diam. Hypanthium rugose and glandular, each gland often in a broad pit, usually green except for a reddish summit. Sepals very broadly ovate to elliptic, 2-3.5 mm long, 2.5-3.5 mm wide, the herbaceous part green and red-tinged or reddish throughout; petaline margin 0.3-0.7 mm wide, usually white at apex and tinged deep pink below. Petals 6-9 mm long, white, persistent. Stamens 30-50 in 2 complete series. Longest filaments 4-6 mm long, united for c. 0.5 mm at base. Anthers 0.4–0.7 mm long. Ovary c. half-inferior or more than half-superior; ovules 6-12 per loculus, horizontal. Style 4-6 mm long. Fruits over half-superior, 3-4.3 mm long. Seeds 1.3–1.6 mm long, 0.5–0.6 mm wide, 0.9–1.1 mm deep including inner protrusion, medium brown, smooth; inner protrusion 0.8–1.1 mm long, 0.2–0.4 mm deep; hilum towards base of inner surface. Chaff pieces crustaceous.

Selected specimens examined. WESTERNAUSTRALIA [localities withheld for conservation reasons]: 6 Nov. 2003, S. Barrett 1156 (PERTH); 20 Nov. 2004, S. Barrett 1182 (PERTH); 13 Oct. 2005, S. Barrett 1426 (PERTH); 3 Jan. 2003, J.A. Cochrane 4438, A. Crawford & J. Wood (K, PERTH); 20 Oct. 2002, M. Hislop 2840 (AD, PERTH).

Distribution and habitat. Occurs in the western, central and south-eastern parts of the Stirling Range (Figure 5C), on rocky slopes or summits of mountains.

Phenology. Flowers from September to November. Mature seeds recorded in December and January. The leaves tend to turn reddish during summer.

Conservation status. Priority Three under DEC Conservation Codes for Western Australian Flora (Smith 2012). Known from many localities, all within a large national park, including some recent collections, over a range c. 45 km long.

Affinities. This taxon possibly should be treated as a subspecies of *H. myrtifolium* (see notes under that species). *Hypocalymma phillipsii* can be readily recognised, however, as it is the only member of sect. *Cardiomyrtus* to have hairs on its young stems. Some species of sect. *Hypocalymma* also have hairy stems but their hairs are often compressed, longer and acute, and they may also be branched.

Notes. While there are normally two flowers in an axil in *H. phillipsii*, there is no clear peduncle and the axis may grow out between the two flowers, which then appear to be solitary on each side of the new axis, each subtended by a small leaf-like bract or reduced leaf as well as the large main subtending leaf.

Hypocalymma speciosum Turcz., *Bull. Cl. Phys.-Math. Acad. Imp. Sci. Saint-Pétersburg* 10: 332 (1852). *Type*: 'Nova Hollandia' [Stirling Range, Western Australia], 1848, *J. Drummond* 5: 119 (*holo*: KW; *iso*: BM 00105087, K 000797331, MEL 104628, 104629, PERTH 01829599).

Hypocalymma boroniaceum F.Muell. ex Benth., *Fl. Austral*. 3: 95 (1867). *Type*: Swan River Colony [Stirling Range, Western Australia], 1848, *J. Drummond* 5: 119 (*lecto*: K 000797331, here selected; *isolecto*: BM 00105087, K, KW, MEL 104628, 104629, PERTH 01829599).

Illustration. W.E. Blackall & B.J. Grieve, How Know W. Austral. Wildflowers 3A: 91, n. 10 (1980).

Shrub 0.25–0.7 m high, often producing multiple erect stems from a lignotuber. Young stems 4-angled and somewhat 4-winged, glabrous; wings up to 0.4 mm wide. Petioles ± absent. Leaf blades antrorse or patent, cordate or ovate or circular, 4–18 mm long, 7–15 mm wide, ± entire; midrib level on upper surface and not very prominent on lower surface. Inflorescence commonly occupying 3–8 adjacent nodes on each branchlet. Peduncles almost absent or up to 1.5 mm long, 1–4-flowered, often pendulous. Secondary axes 6–12 mm long. Bracteoles usually deciduous, obovate in outline, 2–3.3 mm long, obtuse, somewhat scarious. Pedicels absent or very reduced. Flowers mostly 10–12 mm diam. Hypanthium markedly rugose-pitted, green or red-tinged. Sepals broadly elliptic, 2–3.8 mm long, 2.3–2.7 mm wide, with a green or reddish, rugose herbaceous part; petaline margin 0.3–0.5 mm wide, white, tinged with red. Petals 6–7 mm long, deep pink-purple, persistent. Stamens 25–40 in 2 series, forming a complete ring. Longest filaments 3.5–4.5 mm long, united at base for c. 0.3 mm. Anthers c. 0.4 mm long. Ovary superior, often pinched in at base; ovules 2 per loculus, erect. Style 3–4 mm long. Fruits superior, c. 3 mm long. Seeds c. 1.65 mm long, c. 0.5 mm wide, c. 1 mm deep, very pale brown, minutely colliculate; inner protrusion c. 1.2 mm long, c. 0.35 mm deep; hilum slightly below middle of seed. Chaff pieces crustaceous.

Selected specimen examined. WESTERN AUSTRALIA [locality withheld for conservation reasons]: 13 Dec. 1988, *R.T. Wills* 970 (PERTH).

Distribution and habitat. Occurs in rocky soils in the central and western parts of the Stirling Range (Figure 5D). Hypocalymma speciosum overlaps in range with both H. phillipsii and H. myrtifolium and seems to occur in similar habitats so it possibly sometimes grows with them.

Phenology. Flowers from September to December. Mature fruits recorded in December.

Conservation status. Recently listed as Priority Two under DEC Conservation Codes for Western Australian Flora (Western Australian Herbarium 1998–). No collections have been made of *H. speciosum* since 1994 but its distribution is well known from earlier collections. Its localities are scattered over a distance of at least 35 km, all within a large national park.

Affinities. This species is very distinctive. It shares some morphological characters with the other two species that occur in the Stirling Range and the molecular data suggest that its relationship lies with them (see Figure 1). However, it is keyed out with the geographically distinct species *H. cordifolium* and *H. minus* as it is similar to them in leaf shape and ovule number. The ovary is almost fully superior in *H. speciosum*; the superior part is about 2 mm long and usually pinched in below the fully superior ovules, with only the sterile base being adnate to the short hypanthium. The superior ovary of *H. speciosum* is unique in the Chamelaucieae; most members of the tribe have a fully or largely inferior ovary, while others, including the other four members of sect. *Cardiomyrtus*, have a more or less half-inferior ovary.

Typification. Bentham cited two syntypes for *Hypocalymma boroniaceum*: a primary one collected by Drummond and a secondary one collected by Dutton. There are three Drummond duplicates at Kew, one stamped 'Herbarium Benthamianum 1854', one stamped 'Herbarium Hookerianum 1867', and one ex herb. W.W. Saunders with a sticker saying it was 'Presented by the Linnean Society, 1915'; all sheets have ample flowering material. Duplicates in BM and G bear no evidence of examination by Bentham. At MEL, there is one Drummond sheet (MEL 104628) as well as the Dutton collection (MEL 104629); only the Dutton collection is marked to indicate that it was sent to Bentham. For the same reasons given under *H. hypericifolium*, we have chosen the specimen ex Herbarium Benthamianum as lectotype.

Notes. James Drummond was sufficiently impressed by this species to describe it in a letter to G. Leake on 29 October 1948 as 'a beautiful species of the *Cardiomyrtus* section of the genus which I observed on the Toolbrunup Hills' (Drummond 1839–1848).

Hypocalymma speciosum has deeply coloured, pink-purple flowers, which are often pendulous. Pollinator observations of this taxon are needed to assess the function of these characters. The apparent length of the style is increased by its position on the superior ovary.

More fruiting collections with mature seeds are needed for this species as only one mature seed has been seen so far.

Hypocalymma sect. Verticilla Rye, sect. nov.

Fruticuli pusilli. Caules juvenes 3-angulati, 3-porcati, verticillis 3-foliatis. Flores solitarii e foliorum summorum axillis orientes. Pedunculi longi. Bracteolae 2, oppositae, deciduae. Petala 5, sepala multi superantia. Stamina plerumque 17–25, pro longitudine plus dimidium in circulum completum conjuncta, saepe longa et brevia alternata. Filamenta compressa, apicem versus decrescentia. Antherae basifixae, dehiscentia parallela longitudinali; glans connectiva simplex, dorsalis et subterminalis. Ovarium 3-loculare; ovula 1–10 per loculum. Styli basis in depressionem cylindricum immersa. Fructus: capsula 3-valvata, c. 1/2 inferior. Semina crustacea, corpo ad basim lato, ad apicem angustiore in dimidio distali tumore elaisomo expanso, 1–1.3 mm longa, alba vel brunnea.

Typus: Hypocalymma verticillare Rye.

Shrubs (where known) 0.2–0.8 m high, single-stemmed, with very slender stems. Leaves in alternating whorls of three, antrorse to patent, mostly widely spreading. Petioles short but well defined. Leaf blades discolorous, small, with recurved to revolute margins; abaxial surface pale green, oil glands in several main rows on each side of a prominent midvein; adaxial surface significantly darker green

than abaxial surface, with oil glands inconspicuous. Flowers solitary in the upper leaf axils, pendulous. Peduncles long, 1-flowered. Bracteoles 2, opposite, caducous or deciduous, small and very narrow, entire, inconspicuous. Pedicels much shorter than peduncles. Hypanthium with adnate part conic and free part often becoming ± flat. Sepals 5, erect, persistent in fruit, entire, not or somewhat ridged along middle of the more herbaceous part. Petals 5, spreading or erect, deciduous or persistent in fruit, almost circular, shortly clawed, white or possibly sometimes pink. Staminodes absent or up to 5. Stamens c. 17–23 united into a broad cylinder that contracts (becomes narrower) towards the top, the longest stamens either tending to be opposite the sepals or not showing any particular position with respect to the sepals and petals but always tending to alternate with short stamens around the circle, sometimes with anthers of very different sizes present. Filaments united for about half to all of their length, very compressed where united into the ring and either compressed or very narrow where free. Anthers sub-basifixed; cells free from one another, parallel, longitudinally dehiscent; connective gland simple, dorsal and subterminal. Ovary partly superior, 3-locular, summit hidden from side view by the androecium; placentas axile, sessile, broadly elliptic to circular, broadly attached at centre; ovules solitary and erect or up to 10 per loculus and radially arranged. Style terete, slender, with base immersed in a cylindrical depression at centre of ovary; stigma capitate or peltate. Fruits about half-inferior where known, surrounded by the persistent androecium, thick-walled; valves rounded, usually rugose. Seeds often many per fruit, crustaceous, the body ovoid-reniform, i.e. broader below the middle, but upper part expanded by an inner protrusion, 1–1.3 mm long, smooth, shiny; inner protrusion distal to the hilum, whitish; hilum towards base of inner surface. Chaff pieces scarcely known, sometimes absent.

Size and distribution. A section of two species, endemic to Western Australia, with an incompletely known range in the far south-west of the State. *Hypocalymma verticillare* is recorded from north of Walpole, occurring near the margin of a wetland in a region of very high rainfall. Like that species, *H. connatum* has discolorous leaves, a character that occurs in some species of Chamelaucieae from the wettest parts of the south-west but is virtually unknown in areas of moderate rainfall. One possibility recorded in a note on the 'rare file', dated 1995, is that *H. connatum* came from the Katanning–Cranbrook–Tambellup area on the train line, one of the likely sources of plants for a wildflower show in the 1930s.

Etymology. From the Latin verticillus (whorl, circle), referring to the whorled leaves of this section.

Notes. The rather large degree of morphological separation of the two known species suggests that much greater variation may have existed when sect. *Verticilla* reached its peak of speciation long ago. Nevertheless there are striking similarities between the two species described below and they are very readily distinguished from the other sections of *Hypocalymma* (see Table 1). Unique characteristics of sect. *Verticilla* include its 3-angled young stems with three rounded ridges and its regularly whorled leaves. It is also unusual in its rather pendulous flowers and fruits, a character also found in one species (*H. speciosum*) of sect. *Cardiomyrtus*. How this character relates to pollination needs to be investigated.

Hypocalymma connatum Strid & Keighery, *Nord. J. Bot.* 22: 572. *Type*: Wildflower Show, Perth, Western Australia, September 1935, *C.A. Gardner s.n.* [original locality and collector unknown] (*holo*: PERTH 04231457).

Shrub height unknown but at least 0.4 m. Young stems with internodal ridges that are c. 0.6 mm thick at summit; minor lateral branchlets strongly compressed up to the first node but obviously 3-ridged above this node. Leaves moderately antrorse to patent. Petioles c. 0.5 mm long. Leaf blades narrowly ovate, 6–7 mm long, 1–1.5 mm wide, acute, with strongly recurved or revolute margins, often with a

pale triangular apical point up to 0.5 mm long; abaxial surface with 2 or 3 main rows of usually 8–15 oil glands on each side of the midvein. *Inflorescence* occupying 1 or 2 nodes per branchlet. *Peduncles* strongly curved at base to be pendulous in fruit, 1-flowered, 3-4 mm long, somewhat compressed. Bracteoles apparently very small. Pedicels 0.7–1 mm long. Flowers not seen at anthesis but probably pendulous, certainly becoming pendulous. Hypanthium c. 1.5 mm long and 4.5 mm diam. in fruit, irregularly narrowly wrinkled longitudinally and with oil glands visible; free portion apparently absent in fruit. Sepals very broadly or depressed ovate, 2–2.5 mm long, up to c. 3.2 mm wide, broadly obtuse, somewhat ridged in bud but not at all ridged in fruit; thin-textured margin narrow, whitish or red-tinged. Petals 3.5-4 mm long, probably white, persistent, erect in fruit. Stamens c. 17. Longest filaments c. 3 mm long, united for half or over half their length, the free part flattened but tapering to a narrow apex. Anthers all fertile, all of a similar size in each flower, the smallest c. 0.35 mm long, the largest c. 0.4 mm long. Style 3.5–4 mm long; stigma capitate, c. 0.2 mm diam. Ovary probably largely inferior; ovules reportedly 3 or 4 but probably 8-10 per loculus. Fruits half-inferior, c. 3.5 mm long, c. 4.5 mm diam. Seeds 1–1.1 mm long, c. 0.5 mm wide, 0.5–0.6 mm thick, medium brown; inner protrusion extending down from top of seed for more than half the length of the seed body, c. 0.75 mm long, c. 0.25 mm deep, whitish. (Figures 4C, 6)

Distribution and habitat. Unknown, but presumably the species occurs either in a similar high-rainfall area to, or in a slightly drier area than, *H. verticillare* (see under *Size and distribution* above).

Phenology. Mature fruits recorded in September.

Conservation status. Priority One under DEC Conservation Codes for Western Australian Flora (Smith 2012). Being known from a single old collection of unknown locality, this species was presumed by Strid and Keighery (2002) to be extinct.

Affinities. Strid and Keighery (2002) thought their new species was probably related to *H. myrtifolium* Turcz., a member of the sect. *Cardiomyrtus*. Now the newly described species *H. verticillare* is known to be a much closer match in its morphology to *H. connatum*.

Notes. The habit of *H. comnatum* is unknown, but the plant sampled was likely to have been at least 0.4 m high as that was the length of the apparently erect branch mounted on the herbarium sheet. Bracteoles had fallen from the few late flowers and fruits that were in a packet attached to the sheet, but there was a very short, apparently shrivelled structure *c*. 0.35 mm long at the top of the peduncle of the single flower left attached to the mounted branch. It seems likely that bracteoles would normally be larger, so this measurement was not given in the description above. Although the fruits were empty, some seeds and one piece of chaft were preserved in a packet.

Adding to the mystery surrounding the origin of this plant are the notes and illustration of morphological characters provided on the specimen by Charles Gardner (Figure 6). Notes indicate that there are '3 or 4 ovules in each cell app. collateral' and these are drawn as being erect. In fact, there appear to be eight to ten ovules in each cell, judging from the number of attachment points on the placentas in the fruits and from the number of indentations formed by seeds inside the fruit wall of each loculus. Perhaps the particular fruit examined by Gardner had most of the seeds already dispersed and only three or four seeds were left, giving the impression that the ovule number was low.

Seeds of *H. verticillare* are fully erect, solitary, off-white and fairly smooth but not particularly shiny, whereas those of *H. connatum* are more numerous, probably closer to horizontal,

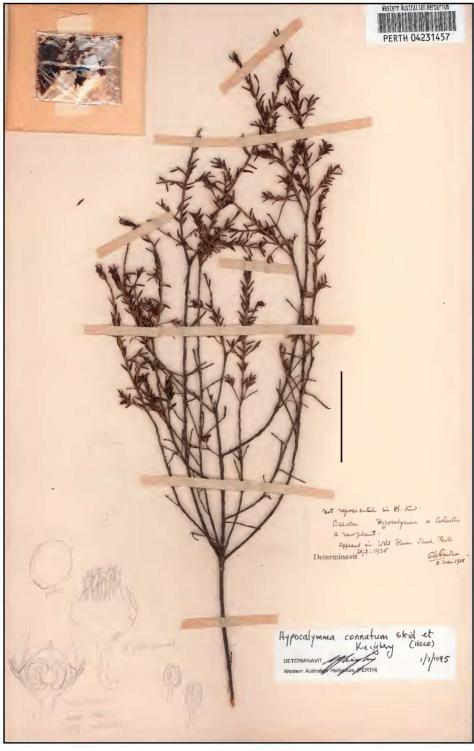


Figure 6. Holotype of *Hypocalymma connatum*. Scale bar 5 cm.

medium brown, very smooth and very shiny. Chaff pieces are apparently absent or few in *H. connatum* as only one could be found in the loose seed sample on the holotype; also, the depressions in the fruit wall suggest that it is mostly seeds that have been produced. The single chaff piece examined was compressed but crustaceous, and most of its surface was darker than the seeds although its very reduced inner protrusion was paler.

Hypocalymma verticillare Rye, sp. nov.

Hypocalymmate connato affinis sed foliis minoribus latioribusque, floribus minoribus, staminibus magis variabilibus, ovulis in quoque loculo solitariis et stigmate peltato differt.

Typus: north-east of Walpole, Western Australia [precise locality withheld for conservation reasons], 12 May 2005, *B.L. Rye* 250504 & *E.D. Middleton* (holo: PERTH 07131232; iso: CANB, K, MEL, NSW).

Hypocalymma sp. Walpole (E.D. Middleton EDM 33), Western Australian Herbarium, in *FloraBase*, http://florabase.dec.wa.gov.au [accessed March 2013].

Shrub 0.2–0.8 m tall, single-stemmed at base, much branched above, with slender stems. Young stems with ridges c. 0.3 mm thick at top end. Leaves very widely antrorse or patent. Petioles 0.3-0.5 mm long. Leaf blades ovate to elliptic or becoming narrowly so by recurving of the margins, 3-6 mm long, 1.8-2.3 mm wide, acute or obtuse, with strongly recurved or revolute margins, the apex a very reduced point; abaxial surface pale green, with 2 or sometimes 3 main rows of usually c. 6 oil glands; adaxial surface olive-green, with oil glands inconspicuous. Inflorescence occupying 1-5 nodes per branchlet (the fertile nodes not always consecutive), with up to 3 but often only 1 or 2 flowers per node. Peduncles spreading, straight or somewhat recurved, 2-3.5 mm long, almost terete. Bracteoles caducous or deciduous, incurved to a very narrow shape, linear in outline, 0.5–0.7 mm long, acuminate, reddish. Pedicels 0.7-1.2 mm long. Flowers 5-6 mm diam. Hypanthium with adnate part obconic and free part horizontal, c. 0.6 mm long, 1.8-2.2 mm diam., often reddish. Sepals depressed ovate, c. 0.7 mm long, c. 1.3 mm wide, broadly obtuse, the herbaceous part dark red and somewhat thickened; thin-textured margin narrow, whitish. Petals widely spreading, concave on upper surface, 2-2.5 mm long, white, deciduous in fruit. Staminodes (2-)5, antipetalous, c. 0.15 mm long. Stamens 17-23, with 2-5 opposite each sepal, the longest ones tending to be opposite the sepals but alternating with shorter stamens, the shortest filaments united for all or nearly all their length. Longest filaments 1.5-2 mm long, united for about half their length, the free part filiform. Anthers very varied in size in each flower, the smallest ones infertile (on the staminodes) and c. 0.15 mm long, the largest c. 0.4 mm long and all intermediate sizes also present. Ovary about half-inferior, summit prominently 3-lobed; ovules erect, 1 per loculus. Style slender, 1.4–1.7 mm long; stigma peltate or almost peltate, 0.15–0.2 mm diam. Fruits c. two-thirds-superior, c. 1.8 mm long, c. 2.3 mm wide. Seeds usually formed from the single ovule in each loculus (i.e. no chaff present), erect, 1.1–1.3 mm long, c. 0.4 mm wide, 0.5–0.6 mm deep including inner protrusion, off-white; inner protrusion extending down from top of seed for less than half the length of the seed body, 0.3–0.5 mm long, 0.25–0.3 mm deep. (Figures 2B, 3)

Selected specimens examined. WESTERN AUSTRALIA [all from type locality]: 1 May 1997, E.D. Middleton EDM 33 (PERTH); 29 Mar. 2005, E.D. Middleton EDM 702 (AD, BRI, NSW, PERTH); 12 May 2005, B.L. Rye 250505, 250506 & E.D. Middleton (PERTH).

Distribution and habitat. Known from a single locality between Lake Muir and Walpole (Figure 5D), recorded close to a peat swamp, growing with a variety of myrtaceous species including *Beaufortia sparsa*, *Taxandria parviceps*, *Homalospermum firmum* and *Astartea arbuscula* and with a wide variety

of other taxa such as Adenanthos obovatus, Acidonia microcarpa and Anarthria scabra.

Phenology. Flowers recorded March to May and fruits in May.

Insect associations. Black scales seen on the undersurface of the leaves are very compressed, with a slight ridge along the centre of the exposed dorsal surface, and have a continuous white border (Figure 2B).

Conservation status. Listed by Smith (2012) as Priority Two (DEC Conservation Codes for Western Australian Flora) under the name H. sp. Walpole (E.D. Middleton EDM 33). This species, known from a single locality, was common on the road verge, apparently favoured by disturbance, but few plants were visible in the thick, adjacent vegetation of sedges and low shrubs.

Etymology. As for the section, the epithet refers to the whorled leaves in this species.

Affinities. Differs from the other member of sect. *Verticilla*, *H. connatum*, in its smaller, broader leaves with a very reduced apical point, smaller flowers, more variable stamens, lower ovule number and peltate stigma. It also seems to have more spreading leaves.

The first specimen of *H. verticillare*, collected in 1997, was housed for several years in *H. minus* (as *H. cordifolium* subsp. *minus*). The new species occurs within the range of *H. minus* in a similar damp habitat, and has leaves of a similar shape and colour. The two species show all the differences that separate the sections *Cardiomyrtus* and *Verticilla*, with particularly striking differences in their androecium. *Hypocalymma verticillare* is unique in the genus in having very large differences in the sizes of its anthers and in having a number of solitary, very short, antipetalous staminodes, in addition to the small, moderate-sized and large stamens occurring in groups of two to five opposite the sepals. Directly opposite each sepal there is usually either a moderate-sized stamen (with a large stamen on each side of it), or a single long stamen (bordered by shorter stamens), but there are never more than two large stamens per sepal. While the thecae of the large and small anthers differ markedly in size, the connective gland does not differ much; it is about as large as each of the thecae on the staminodes but greatly exceeded in length by the thecae of the largest anthers.

Notes. The free part of the hypanthium is more or less horizontal so does not increase the length of the hypanthium to any significant degree but contributes greatly to its width. Each loculus of the ovary contains an almost sessile placenta, which is broadly attached at the centre. In *H. verticillare* the stigma barely protrudes from the ovary summit at the stage of pollen release from the anthers although it is well exserted by the fruiting stage (Figure 3C). Figure 3B shows the stigma at an intermediate stage.

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References

- Bentham, G. (1867). Flora Australiensis. Vol. 3. (Lovell Reeve & Co.: London.)
- Berg, R.Y. (1975). Myrmecochorous plants in Australia and their dispersal by ants. Australian Journal of Botany 23: 475–508.
- Blackall, W.E. & Grieve, B.J. (1980). *How to know Western Australian wildflowers*. Part 3A. Revised 2nd edn by B.J. Grieve. (University of Western Australia Press; Nedlands.)
- Briggs, B.G. & Johnson, L.A.S. (1979). Evolution in the Myrtaceae evidence from inflorescence structure. Proceedings of the Linnean Society of New South Wales 102: 157–256.
- Brown, E.M., Burbidge, A.H., Dell, J., Edinger, D., Hopper, S.D. & Wills, R.T. (1997). *Pollination in Western Australia: a database of animals visiting flowers*. Handbook No. 15. (WA Naturalists' Club: Perth.)
- Bureau of Meteorology (2013). http://www.bom.gov.au/jsp/ncc/climate_averages/rainfall/index_jsp [accessed 27 February 2013].
- Department of the Environment, Water, Heritage and the Arts (2008). *Interim Biogeographic Regionalisation for Australia (IBRA) Version 6.1*. http://www.environment.gov.au/parks/nrs/science/bioregion-framework/ibra/index.html [accessed 26 April 2013].
- Drummond, J. (1839–1848). Copies of most of James Drummond's letters in Kew Library with extracts from Hooker's publications of them in his botanical journals for comparison, arranged in chronological order, not as bound in Kew vols.
- Elliot, W.R. & Jones, D.L. (1990). Encyclopaedia of Australian plants suitable for cultivation. Vol. 9 [Gr–JZ]. (Lothian Publishing Co. Pty Ltd: Melbourne.)
- Endlicher, S.L. (1837). Myrtaceae. *In*: Endlicher, S.L., Bentham, G., Fenzl, E. & Schott, H.W. *Enumeratio plantarum*. pp. 46–51. (Fr. Beck: Vindononae.)
- Endlicher, S.L. (1840). Genera plantarum. Part 16. (Fr. Beck: Vindononae.)
- Foster, J.E. (1996). Cladistic and biogeographic analysis of the genus *Hypocalymma* (Endl.) Endl. (Myrtaceae). Diploma of Science thesis. University of Western Australia.
- Hopper, S.D. & Gioia, P. (2004). The Southwest Australian Floristic Region: evolution and conservation of a global hot spot of biodiversity. Annual Review of Ecology, Evolution and Systematics 35: 623–650.
- Houston, T.F. (2000). *Native bees on wildflowers in Western Australia*. Special Publication No. 2. (Western Australian Insect Study Society Inc.: Perth.)
- Johnson, L.A.S. & Briggs, B.G. (1984). Myrtales and Myrtaceae a phylogenetic analysis. *Annals of the Missouri Botanical Garden* 71: 700–756.
- Lam, N., Wilson, Peter G., Heslewood, M.M. & Quinn, C.J. (2002). A phylogenetic analysis of the *Chamelaucium* alliance (Myrtaceae). *Australian Systematic Botany* 15: 535–543.
- Main, A.R. (1981). Plants as animal food. *In*: Pate, J.S. & McComb, A.J. (eds) *The biology of Australian plants*. pp. 342–360. (University of Western Australia Press: Nedlands, Western Australia.)
- Niedenzu, F. (1893). Myrtaceae. *In*: Engler, A. & Prantl, K. (eds) *Die natürlichen Pflanzenfamilien*. Vol. 3(7), pp. 57–105. (Englelmann: Liepzig.)
- Patel, V.C., Skvarla, J.J. & Raven, P.H. (1984). Pollen characters in relation to the delimitation of Myrtaceae. Annals of the Missouri Botanical Garden 71: 858–969.
- Pike, K.M. (1956). Pollen morphology of Myrtaceae from the south-west Pacific area. Australian Journal of Botany 4: 13-53.
- Rye, B.L. (2010). A lectotype and new combination in *Hypocalymma* (Myrtaceae: Chamelaucieae). *Nuytsia* 20: 323–326.
- Rye, B.L. (2013). A revision of the south-western Australian genus Astartea (Myrtaceae: Chamelaucieae). Nuytsia 23: 189–269.
- Rye, B.L. & Trudgen, M.E. (2008). Seorsus, a new Gondwanan genus of Myrtaceae with a disjunct distribution in Borneo and Australia. Nuytsia 18: 235–257.
- Schauer, J.C. (1844). Myrtaceae R.Br. In: Lehmann, J.G.C. (ed.) Plantae Preissianae. Vol. 1, pp. 96-158. (Meisner: Hamburg.)
- Slater, J.A. (1975). On the biology and zoogeography of Australian Lygaeidae (Hemiptera: Heteroptera) with special reference to the southwest fauna. *Journal of the Australian Entomological Society* 14: 47–64.
- Slater, J.A. (1976). The biology, distribution and taxonomy of some Lygaeidae of southwest Australia (Hemiptera Heteroptera). *Journal of the Australian Entomological Society* 15: 129–151.
- Smith, M.G. (2012). Threatened and Priority Flora list for Western Australia. (Department of Environment and Conservation: Kensington, Western Australia)
- Strid, A. & Keighery, G.J. (2002). A taxonomic review of Hypocalymma (Myrtaceae). Nordic Journal of Botany 22: 535–572.
- Sweedman, L. & Merritt, D.J. (eds) (2006). Australian seeds: a guide to their collection, identification and biology. (CSIRO Publishing: Victoria.)

Thornhill, A.H., Wilson, Peter G., Drudge, J., Barrett, M.D., Hope, G.S., Craven L.A. & Crisp, M.D. (2012). Pollen morphology of the Myrtaceae part 3: tribes Chamelaucieae, Leptospermeae and Lindsayomyrteae. *Australian Journal of Botany* 60: 225–259.

- Trudgen, M.E. (1986). Reinstatement and revision of Rinzia Schauer (Myrtaceae, Leptospermeae, Baeckeinae). Nuytsia 5: 415–439.
- Turczaninow, N. (1862). Decas octava. Generum adhuc non descriptorum. Bulletin de la Société Impériale des Naturalistes de Moscou 35(4): 321–325.
- Western Australian Herbarium (1998–). FloraBase—the Western Australian flora. Department of Environment and Conservation. http://florabase.dec.wa.gov.au [accessed 26 April 2013].
- Wilson, Peter G., Heslewood, M.M., Lam, N. & Quinn, C.J. (2004). Progress towards a phylogeny of the *Chamelaucium* alliance (Myrtaceae). *Australian Biologist* 17: 28–33.
- Wilson, Peter G. & Heslewood, M.M. (2011). Myrtaceae: progress on all fronts. XVIII International Botanical Congress (IBC 2011) Abstract Book. pp. 326–327.
- Woodward, T.E., Evans, J.W. & Eastop, V.F. (1970). Hemiptera. *In: The Insects of Australia*. pp. 387–457. (Melbourne University Press: Melbourne.)